

Neural Basis of Semantic Memory

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Neural foundations for conceptual representations: Evidence from functional brain imaging

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12.1 Overview

Semantic memory refers to a major division of declarative memory that includes knowledge of the meaning of objects and words. This chapter will focus on one aspect of the functional neuroanatomy of semantic memory: the representation of the meaning of concrete objects and object properties. The initial motivation for our work on this topic was reports of patients with so-called category-specific knowledge disorders — specifically, patients with relatively selective impaired knowledge about animals and other animate objects, and those with relatively selective impairments for man-made, inanimate objects such as tools. Since the publication of the seminal case studies by Warrington and colleagues (Warrington & McCarthy, 1983; Warrington & Shallice, 1984), well over 100 patients have been reported with a category-specific deficit for biological categories (living things, especially four-legged animals), relative to inanimate objects (especially tools and other artifacts), and more than 25 cases with the opposite pattern of deficit (Capitani *et al.*, 2003). Our work has been motivated by an appreciation of the importance of these clinical cases for understanding the organization of conceptual knowledge, object recognition, and storage of long-term memories. In this chapter I shall outline a model of how conceptual knowledge about concrete entities (objects) is organized in the brain based on functional brain imaging studies of normal, intact individuals. From a theoretical perspective, the model attempts to incorporate the main features of property-based models that have dominated thinking about category-specific disorders for over one hundred years, and the challenge to this view from the

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Domain Specific theory (Caramazza & Shelton, 1998; for an overview of recent theories of the organization of conceptual knowledge in the brain see Caramazza, 1998; Martin & Caramazza, 2003). The model I will outline, The Sensory–Motor Property Model for Representing Domain-Specific Information – which I shall refer to simply as the sensory–motor model – is consistent with recent attempts to accommodate the functional brain imaging and neuropsychological evidence (Caramazza & Mahon, 2003). I shall concentrate on the two broad domains of knowledge, the first is the representation of animate agents – living things that move on their own; the second is ‘tools’ – man-made manipulable objects for which there is a direct relationship between how an object is manipulated and its function. However, the model is relevant for understanding other object domains as well, such as place (Epstein & Kanwisher, 1998), food (Crutch & Warrington, 2003; Simmons *et al.*, 2005), and number (Dehaene *et al.*, 1999).

12.2 The expression and representation of knowledge

Before proceeding, a number of preliminary issues need to be addressed. First is the issue of knowledge expression. There is no need for any organism to acquire information unless that information can be expressed. Organisms learn, and the evidence for that learning is demonstrated by a change in behavior. What is represented (stored) in the brain is information. What is expressed is knowledge. How this knowledge is expressed is of fundamental importance for understanding how information is represented. For humans, a primary, and arguably *the* primary, mode of expression is via the language system. Questions designed to probe knowledge about a specific entity are posed orally or in written form and subjects respond verbally. Occasionally, a manual response may be required (e.g. show me how you would use a hammer) either by actually manipulating the object or via pantomime. However, regardless of whether the response is verbal or manual, knowledge is expressed explicitly. This explicit knowledge is typically referred to as associative knowledge or encyclopedic knowledge, and it is this level of knowledge representation that is typically probed in both normal and brain-damaged individuals. Associative or encyclopedic knowledge has three main characteristics. First, as noted above, retrieval is explicit. Second, there is no intrinsic limitation on the amount of information that can be stored and retrieved. For a specific category of objects (e.g. *dogs*), we may know lots of things. We know they are living things, have four legs, are smaller than a car, like to take walks, like to play fetch, are considered pets in many parts of the world, show up on the menu in other parts of the world, and so on, and so on. Moreover, it does not matter whether the information is true. If you believe that dogs can fly, then that information is

part of your semantic knowledge about dogs and represented somewhere in the brain. Finally, this level of knowledge is idiosyncratic. Some people know lots about dogs, while others know very little.

This explicitly expressed knowledge about objects can be contrasted with a different level of object concept representation referred to as core properties or “semantic primitives” (Martin, 1998). In contrast to encyclopedic knowledge, semantic primitives are accessed implicitly and automatically in the service of comprehension, are highly constrained in number, and are universal. This level of representation allows us to quickly and efficiently identify objects and understand words, and forms the foundation for our vast stores of encyclopedic knowledge about objects. While the model to be described here does not address the organization of encyclopedic knowledge, it makes strong claims about the organization of semantic primitives with regard to both their representational content and organization in the brain.

In the sensory–motor model, the concept of an object is composed of semantic primitives that represent those properties of the object that allow for fast and efficient recognition. For example, the properties associated with common tools include stored representations of what they look like, how they move when used, and how they are manipulated. These primitives are stored within the same neural systems active when we learned about those properties. Specifically, they are stored within visual processing systems for perceiving object form and object motion, and action systems responsible for visuomotor transformations and for grasping and manipulating objects.

12.3 What we have learned from functional brain imaging about the representation of object properties and categories

First, I’ll provide a brief overview of findings from functional brain imaging studies. Many of these findings have been reviewed in detail previously (e.g. Martin, 2001; Martin & Chao, 2001; Joseph, 2001; Bookheimer, 2002; Thompson-Schill, 2003).

1. *Conceptual processing of objects, as represented by pictures or words, is associated with activity in a widely distributed network.* The most commonly activated regions are bilateral ventral occipitotemporal and lateral temporal cortices, and left posterior parietal (especially the intraparietal sulcus), ventral premotor, and lateral prefrontal cortices.
2. *Activity within these regions is modulated by category.* Objects belonging to different conceptual categories produce different patterns of activity in these regions. The exception is left lateral prefrontal cortex, which has been

mostly strongly linked to selecting, retrieving, and manipulating semantic information assumed to be stored elsewhere (e.g. Gabrieli *et al.*, 1998; Badre *et al.*, 2005).

- 3. *All object categories tested to date show differential patterns of activity in ventral occipitotemporal cortex.* The most studied objects have been human faces, houses, animals, and tools (e.g. Chao *et al.*, 1999a; Yovel & Kanwisher, 2004). However, distinct object category-related patterns of activity have been reliably discriminated among relatively large sets of object categories (seven by Haxby *et al.*, 2001; seven by Spiridon & Kanwisher, 2002; ten by Cox & Savoy, 2003).
- 4. *Lateral temporal cortex responds to a more limited number of object categories than does ventral temporal cortex.* The most common finding has been activation of the superior temporal sulcus (STS) in response to faces and animals (typically stronger in the right than left hemisphere), and activation of the middle temporal gyrus (MTG) in response to tools (typically stronger in the left than right hemisphere). Objects shown moving in their characteristic fashion produce enhanced, category-related activity in these regions (Beauchamp *et al.*, 2002, 2003).

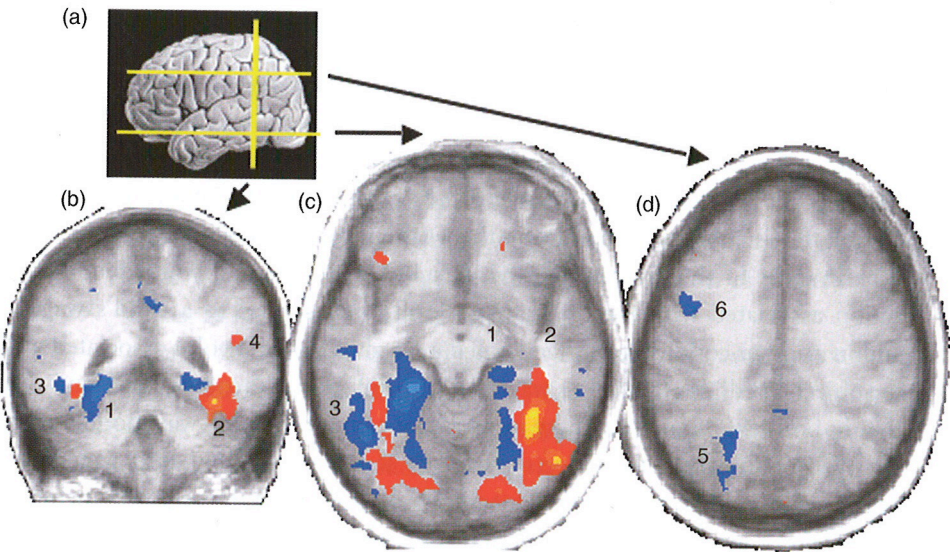


Figure 12.1. Group fMRI activation map showing the location of hemodynamic activity associated with naming pictures of animals (red–yellow spectrum) and pictures of tools (blue–green spectrum). Yellow lines on lateral view of the brain (A) indicate location of the coronal (B) and axial (C, D) slices. 1. Medial region of the fusiform gyrus. 2. Lateral region of the fusiform gyrus. 3. Left middle temporal gyrus, MTG. 4. Superior temporal sulcus, STS. 5. Left intraparietal sulcus. 6. Left ventral premotor cortex. Adapted from Chao *et al.* (2002).

5. *Activation of the intraparietal and ventral premotor cortices has been strongest to tools and other manipulable objects.* This activity is nearly always confined to the left hemisphere (e.g. Chao & Martin, 2000).

Based on these findings and the studies to be reviewed below, two conclusions can be drawn. First, the regions discussed above are involved in both perceiving and representing (storing) information about different object properties such as form (ventral occipitotemporal cortex), motion (lateral temporal cortex), and object use (intraparietal and ventral premotor regions). Second, at least some of these purported object-property regions appear to be organized by superordinate category, as well. This seems most clear for posterior regions of the temporal cortex. In the fusiform gyrus, stimuli depicting animate agents (humans and animals) produce more activity in the lateral portion than manipulable artifacts, while in the medial portion of the fusiform gyrus the opposite bias is found. In lateral temporal cortex, STS responds more to animate objects than to artifacts, while MTG responds more to manipulable artifacts than animate beings (see Figure 12.1 for the location of these regions).

12.4 Retrieving information about object properties: the representation of object-associated motion and object-associated color

In 1995 we reported findings from two experiments using positron emission tomography (PET) (Martin *et al.*, 1995). The paradigm was modeled after the now-classic verb generation paradigm developed by Petersen and colleagues (Petersen *et al.*, 1988). Subjects were presented with achromatic line drawing of objects (in one experiment) or the written names of objects (in the other experiment). In the critical conditions, subjects generated a word denoting an action associated with the object (e.g. “pull” in response to a child’s wagon), and in another condition they generated a word denoting a color associated with the object (“red” for the child’s wagon). One important outcome of this study was that in both experiments activity in posterior temporal cortex was modulated by the type of information subjects retrieved. Relative to color word generation, action words elicited heightened activity in several brain regions, including a posterior region of the left lateral temporal cortex, just anterior to the primary visual motion processing area, MT. It was the location of this activity near MT that initially motivated us to suggest that information about object motion may be stored in this region of the brain.

There are now well over two dozen experiments reporting an association between verb generation and activation of the posterior region of the left lateral temporal cortex, typically centering on MTG. These studies include wide variation

in stimuli, mode of response, and experimental design. In addition, studies have been done in nine different native languages, thus attesting to the robustness and generality of the finding (reviewed in Martin, 2001; and see Shapiro *et al.*, 2006 for a recent functional magnetic resonance imaging (fMRI) study).

In contrast to action word generation, generating color words elicited heightened activity in ventral temporal cortex, centered on the fusiform gyrus, anterior to regions that respond to object form and color, regardless of whether the object is meaningful or not (Malach *et al.*, 1995; Martin *et al.*, 1996, Kanwisher *et al.*, 1997). Using the same logic applied to the action word generation results, we suggested that information about object color may be stored in the region of the fusiform showing greater activity during color than action word generation.

Although color word generation has not received the same attention in the literature as has action word generation, we have replicated this finding in two other studies. The first study sought to identify regions differentially engaged by semantic and episodic memory retrieval (Wiggs *et al.*, 1999). Patterns of activity associated with retrieving information about an object's typical color (the semantic memory task; e.g. responding "brown" to an achromatic drawing of a football) were contrasted with a condition in which subjects retrieved recently learned, novel color-object associations (the episodic memory task; e.g. responding "purple" to a picture of a football). These two memory retrieval conditions were equated for the stimuli used to cue retrieval (object pictures), information retrieved (color words), and accuracy of performance. Each retrieval task was found to be associated with distinct, albeit overlapping, networks. Most relevant for the present discussion, generating words denoting an object's typical color was associated with activity in the same region of the left ventral temporal cortex as identified in our initial studies.

In a second follow-up study, color word generation was evaluated in relation to color naming and color perception (Chao & Martin, 1999). During different PET scans, subjects viewed colored Mondrians and equiluminant, gray-scale versions of those Mondrians to identify color-responsive areas. During other scans subjects were presented with achromatic line drawings of objects embedded in gray-scale Mondrians and appropriately colored line drawings of objects embedded in colored Mondrians, to identify areas associated with object naming, color naming, and color word generation. The main finding was that color word generation activated the same site in left posterior ventral temporal cortex as found in our previous reports. However, retrieving color information did not activate sites in occipital cortex that were active when viewing the colored Mondrians (lingual gyrus).

This later finding was consistent with a study of color–word synesthetes who experience vivid color imagery when hearing words (Paulesu *et al.*, 1995), and with a study of color perception and color imagery in normal subjects (Howard *et al.*, 1998). In both of those studies, color imagery was associated with activation of sites in the ventral temporal lobe nearly identical to those found in our color word generation studies, but not in occipital sites active during color perception (e.g. Zeki *et al.*, 1991). These findings, coupled with clinical reports of a double dissociation between color perception and color imagery in brain-damaged patients (De Vreese, 1991; Shuren *et al.*, 1996), suggest that information about object color is stored in ventral temporal cortex, and that the critical site is close to, but does not include, sites in occipital cortex that selectively respond to the presence of color.

This claim appears to be at odds with the assertion that the same neural systems are involved, at least in part, in perceiving and knowing about specific object attributes. However, in our study (Chao & Martin, 1999), relative to naming colored objects, naming the color of colored objects elicited activity in occipital regions active when passively viewing colored Mondrians, as well as in the more anterior site in the fusiform gyrus of the temporal lobe active during the color word generation task. Thus, when forced to attend to the specific color of an object, more anterior regions of the temporal lobe are active. This finding is consistent with the notion that the same system may be active during perceiving and knowing about a specific object feature or attribute.

Recent fMRI evidence has provided direct evidence for this claim. Beauchamp and colleagues (1999) replicated previous studies showing that activity is limited to the occipital lobes when color perception was tested by passive viewing. However, when a more attention-demanding color perception task was used, modeled after a standard clinical color perception test (Farnsworth–Munsell Color Perception Task), activity associated with perceiving color now extended from occipital cortex into ventral temporal cortex and the fusiform gyrus. Using Beauchamp’s adaptation of the Farnsworth–Munsell Color Perception Task, Simmons and colleagues have now shown that retrieving information about object color – but not object motion – does in fact activate the same region in the fusiform gyrus active when color is perceived (Simmons *et al.*, 2006). Thus these data provide strong evidence that information about a particular object property like its typical color is stored in the same neural system active when colors are actively perceived.

I shall now discuss studies that suggest a relationship between these property-based systems and object categories.

12.5 Property-based neural circuits for representing object categories

In 1996 we reported findings from two PET experiments on the neural systems associated with naming objects from two different semantic categories (animals and tools; Martin *et al.*, 1996). Subjects named line drawings of objects in one study, and object silhouettes in the other study. Both studies yielded similar results. The main findings were that both animal and tool naming elicited bilateral activity in the posterior region of ventral temporal cortex (centered on the fusiform gyrus). In addition, relative to naming tools, naming animals showed heightened activity in the medial region of the occipital cortex. In contrast, relative to naming animals, naming tools yielded heightened activity in the posterior region of the left MTG – overlapping with the activity associated with action word generation – and in left premotor cortex. To account for these findings, we suggested that this activity may reflect the fact that identifying tools is dependent on access to information about how these objects move (left MTG) and how they are manipulated (left ventral premotor cortex).

12.6 Distributed representations for animals, tools, faces, and houses

A surprising and problematic finding from our PET study was that the medial region of the occipital cortex was the only site more active for naming animals than tools. To explain this finding we suggested that it might reflect top–down modulation of early visual areas when access to knowledge about subtle differences in visual properties is needed to distinguish one category member (dog) from another (cat). We rejected the argument that the medial occipital activity was due to greater visual complexity of the animal compared to the tool stimuli based on the findings from the silhouette study (and see Martin, 2001 for a review of studies showing greater occipital lobe activity for animals than tools using words, as well as pictures). The occipital finding, however, was problematic for two reasons. First, if medial occipital activity was driven top–down, then from where did this activity originate? Second, although cases have been reported with impaired knowledge of animals resulting from an occipital lesion (Nielsen, 1958; Tranel *et al.*, 1997), most cases have had lesions of the temporal lobe (Capitani *et al.*, 2003). Thus we turned to fMRI to see if the increased spatial resolution afforded by this imaging modality over PET might reveal more fine-grained category-related differences in patterns of activity. Our first report (Chao *et al.*, 1999a) concentrated on occipitotemporal cortex. Two of the experiments evaluated category-related activity during viewing and delayed match-to-sample with photographs of animals, tools, faces, and houses. Two other experiments evaluated category-related activity by covert naming of photographs of animals

and tools, and by a property verification task using written words to probe knowledge about animals and tools. The main findings were that, in addition to replicating greater occipital lobe activity for animals than tools, category-related differences were noted in the temporal lobes. Specifically, animals (as well as faces) showed heightened, bilateral activity in the lateral region of the fusiform gyrus, while tools (and houses) showed heightened bilateral activity in the medial region of the fusiform gyrus. Recent investigations from a number of other laboratories have shown a similar distinction between the lateral and medial fusiform gyrus for animate and manipulable objects, respectively. For example, Whatmough *et al.* (2002) reported greater activation in the medial fusiform for naming tools than animals, Price *et al.* (2003) reported greater activation of the lateral fusiform for animal pictures relative to tools, and Devlin *et al.* (2005) confirmed the distinction between lateral and medial fusiform for animals and tools using words, rather than pictures, as stimuli. In addition, as in our PET study, we found greater activity in the posterior region of the left MTG for tools than for animals. In contrast, greater activity for animals (and for faces) was found in STS, especially in the right hemisphere.

In the fusiform gyrus there was substantial overlap in the patterns of activity between animals and faces, and between tools and houses. Nevertheless, direct comparison of these categories revealed differences between them, as well. Specifically, animals activated more cortex than faces, and the strongest activity associated with viewing tools was lateral to those associated with houses (see Chao *et al.*, 1999a, for details). These findings suggested that object categories are represented by more elaborate, distributed, and fine-grained networks than revealed by PET. These networks include category-related patterns of activity in both ventral (fusiform gyrus) and lateral (STS, MTG) regions of the posterior temporal cortex.

The regions of posterior temporal cortex that responded more to animals than tools were in areas previously identified as part of the face processing system. Specifically, the lateral occipital gyrus, the lateral region of the fusiform gyrus (the fusiform face area; FFA), and the STS. Activation of the lateral region of the fusiform gyrus in response to human faces relative to other object categories has probably been replicated more times than any other finding in functional brain imaging (for a recent series of elegant studies on faces processing and domain-specificity see Yovel & Kanwisher, 2004). One explanation for this commonality is that the response to animals was not about animals, *per se*, but rather reflected perceptual processing of the animal faces. We directly addressed this issue by contrasting activity during a delayed match-to-sample task with pictures of animals with their faces completely obscured by a white circle, unobscured animals, human faces, and houses (Chao *et al.*, 1999b). The main finding was that

animals with faces and animals without faces showed increased activation in the same lateral fusiform region that showed a greater response to human faces than houses. Moreover, in this region (and in STS) activity associated with animals and faceless animals did not differ. Our results strongly suggest that the response to animals in the lateral fusiform gyrus and STS was not driven by perceptual processes unique to face perception. A similar finding has been reported by Cox *et al.*, who showed that the FFA was active even when human faces were completely occluded (Cox *et al.*, 2004; although see Kanwisher *et al.*, 1999 for contrary evidence).

12.7 The representation of motion properties in the posterior, lateral temporal cortex (MTG, STS)

One of the main assumptions of the sensory–motor account is that activity in lateral temporal cortex reflects properties of motion associated with specific categories of objects. Previous data from studies of monkeys (e.g. Oram & Perrett, 1994) and many functional brain imaging studies of humans (e.g. Puce *et al.*, 1998; Grossman & Blake, 2001) have shown that STS is particularly responsive to biological motion. As noted previously, we have suggested that motion-related information needed to identify manipulable objects is represented in the cortex inferior to STS, specifically in the left MTG and adjoining inferior temporal sulcus. Consistent with this speculation, Tranel and colleagues found that patients with lesions in left MTG (or left intraparietal, or left premotor regions) have selective difficulty naming and retrieving information about tools and their associated actions (Tranel *et al.*, 1997, 2003). However, whether MTG is sensitive to motion, and whether it is differentially sensitive to motion characteristic of non-biological objects, had not been determined. Thus, to directly address this issue, we carried out a series of experiments to test the hypothesis that lateral temporal cortex is differentially sensitive to the motion properties of different object categories.

In the first series of studies, we examined hemodynamic responses to low- and high-contrast moving gratings (used to identify primary motion processing region MT), to biological motion (human figures), and to motion of manipulable objects (tools) (Beauchamp *et al.*, 2002). Three regions in posterior lateral temporal cortex – area MT, STS and MTG – responded to the motion stimuli, and all three areas preferred human and tool motion to moving gratings. As expected, area MT did not show a category bias, with responses here being equally strong for human and tool-related motion. However, anterior and superior to MT in STS, a larger response was observed for human compared

with tool motion, while anterior and inferior to MT in MTG, a larger response was observed for tool motion compared with human motion. Thus these regions showed a strong category-related effect.

We then sought to demonstrate that activity in STS and MTG was related to object-associated motion, rather than simply reflecting the category-related responses observed for static stimuli as found in our previous studies. Subjects performed tasks with both static and moving images. As in the studies reviewed previously, different patterns of category-related activity were noted in the fusiform gyrus, with the lateral portion more responsive to human figures, and the medial portion more responsive to tools. Most importantly, these regions of ventral temporal cortex responded similarly to moving and static objects, even though the moving stimuli were more visually complex and interesting than the static images. Thus ventral temporal cortex showed strong category effects, but these effects were not modulated by motion. In contrast, in addition to a category effect, lateral temporal areas responded much more strongly to moving than static stimuli, supporting the hypothesis that lateral temporal cortex is the cortical locus of complex motion processing (Figure 12.2). These findings also suggest the possibility that these motion sensitive regions have a category-based organization.

In a third experiment, we explored the visual properties underlying the differential sensitivity of STS and MTG to human and tool motion. When humans move, different body parts typically move with complex motion trajectories connected by articulated joints, while tools typically move with simple motion trajectories and few degrees of articulation. We reasoned that if STS prefers flexible, articulated motion, then STS should respond more to humans moving with articulated motion (as during a jumping jack) than to humans moving with unarticulated motion (moving up and down like a hammer). Similarly, if MTG prefers the rigid, unarticulated motion characteristic of tools, it should respond more to unarticulated human motion than to articulated human motion. We constructed stimuli containing humans and tools moving with artificial motion trajectories consisting of simple translation and rotation with no articulation. As predicted, STS preferred humans moving with many degrees of articulation to humans moving with unarticulated motion vectors, while MTG responded more strongly to unarticulated human movements than to articulated human movements. This suggests that the category preferences in STS and MTG may be related to, or emerge from, preferences for different types or patterns of motion (Beauchamp *et al.*, 2002; Beauchamp & Martin, *in press*).

To follow up on these findings, we created stimuli for which information about object category was dependent on an analysis of motion by using point-light

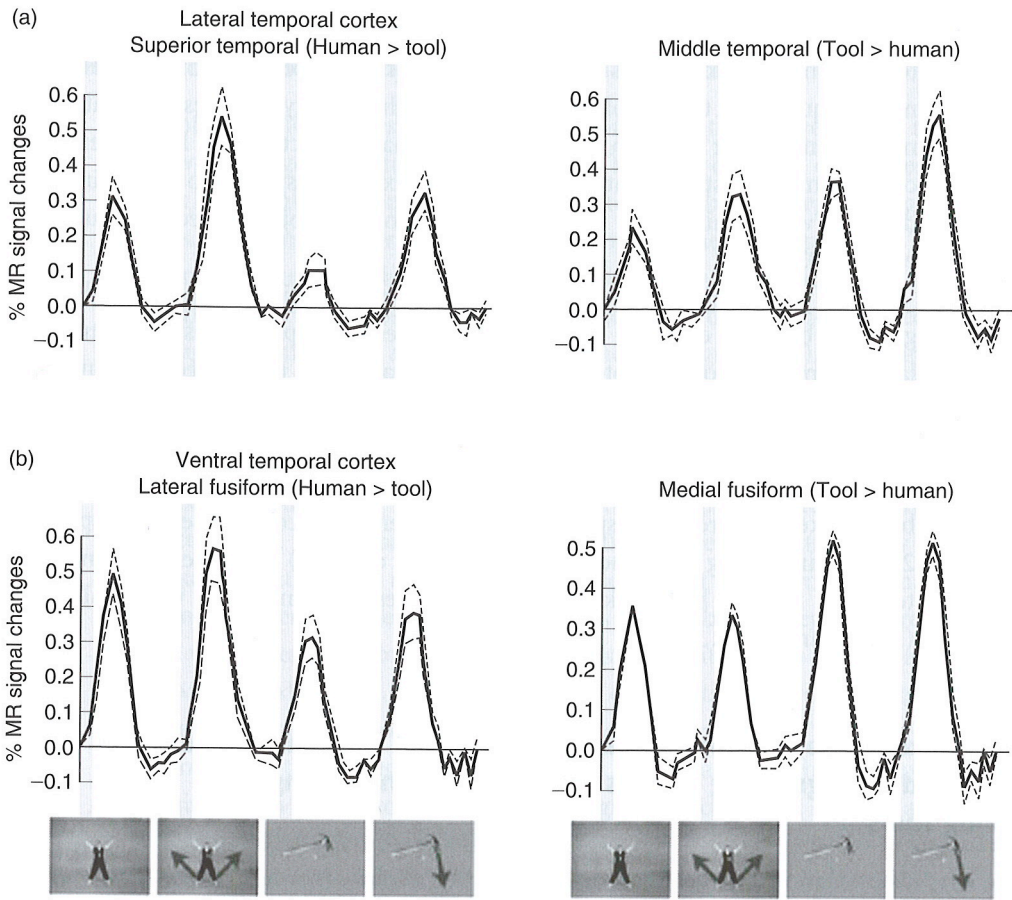


Figure 12.2. Group averaged hemodynamic responses to static and moving humans and tools in (A) lateral and (B) ventral temporal cortices. Vertical gray bars indicate stimulus presentation (2 s). Dashed lines indicate ± 1 SEM. Adapted from Beauchamp *et al.* (2002).

displays (moving dots that are readily interpreted as a single, complex object in motion; Beauchamp *et al.*, 2003). While previous neuroimaging studies examined cortical responses to human point-light displays (e.g. Grossman & Blake 2001, 2002), none compared point-light displays of human motion to point-light displays of tool motion.

Subjects viewed short movies of real objects and point light displays and decided if they depicted a human or a tool. Consistent with our previous studies, real-object and point-light displays of humans elicited stronger activity in the lateral fusiform gyrus and STS than tool stimuli. In contrast, real-object and point-light displays of tools elicited stronger activity in the medial fusiform gyrus, MTG (as well as in left parietal and ventral premotor cortices) relative to human stimuli. Importantly, regions in ventral (lateral and medial fusiform regions) and lateral

(STS and MTG) temporal cortex showed differential responses to human and tool point-light displays. In lateral temporal regions, the responses were nearly equivalent to real-object and point-light displays, suggesting that visual motion, not color or form, is a key determinant of activity in lateral temporal cortex. In contrast, in ventral temporal cortex, the response to the point-light displays was significantly reduced relative to real-object videos (Beauchamp *et al.*, 2003).

Taken together with the previously described studies, these data add to a growing body of evidence on the different response properties of ventral and lateral temporal cortex. Both ventral and lateral cortex responded in a category-related manner (lateral fusiform and STS showing a greater response to human figures than tools, medial fusiform and MTG showing the opposite response pattern). Adding motion had little effect on the responses in fusiform regions, but markedly increased responses in lateral temporal cortex (Beauchamp *et al.*, 2002). Eliminating form and color (point-light displays) had little effect on lateral temporal regions, but markedly reduced the response in ventral temporal cortex (Beauchamp *et al.*, 2003).

12.8 Beyond the temporal lobes: premotor and intraparietal regions associated with grasping objects are active when viewing and naming tools

The relationship between activity in the dorsal stream – particularly in left intraparietal sulcus and left ventral premotor cortex – and the representation of man-made, manipulable objects, has been an very active field of investigation (for review see Johnson-Frey, 2004). Naming photographs of tools, or even simply viewing these pictures, has been shown to elicit enhanced activity for tools in left ventral premotor cortex and in left parietal cortex centered on the intraparietal sulcus, relative to viewing animals, houses, and faces, and relative to naming pictures of animals (Chao & Martin, 2000). These findings are consistent with data from monkey neurophysiology showing that ventral premotor and intraparietal regions contain neurons that respond when the monkey grasps objects and also when seeing objects that they have had experience manipulating (“canonical neuron”; Jeannerod *et al.*, 1995). In the human brain, information about how objects are used may be stored in these regions. As in other regions of the network (medial region of the fusiform gyrus, left MTG), this information may be automatically activated whenever an object is identified (for a recent replication an extension of these findings using words, see Noppeney *et al.*, 2006).

12.9 What do the overlapping patterns of cortical activity mean? Learning-dependent modulation of object category-related activity

All of the fMRI studies from our laboratory and others have shown that regions showing category-related activity respond to many different categories of objects. That is, a region responding maximally to one object category (e.g. preferring tools over animals or faces) is not silent to the “non-preferred” categories (animals, faces). Rather, the response is simply less robust to these other categories. Nevertheless, the activations elicited by these non-preferred categories are significantly above a non-object baseline (see Figure 12.2). There are two views on these weaker activations. In one view they are considered non-specific responses to the presence of any complex visual form. Thus, in this view, weaker activations carry no information about these object categories. This is a necessary assumption if one wants to label a region as face-selective, or tool-selective, etc. (Spiridon & Kanwisher, 2002). The alternative view is that the weaker activations are meaningful in the sense that they carry information about the non-preferred object category. In this view, object categories are associated with widespread, and overlapping, patterns of activity (given the spatial resolution of fMRI; Haxby *et al.*, 2001). A category of objects is represented by the entire pattern of activity, not just by the activity in the region showing a stronger response to this category versus others. We reasoned that an experimental manipulation that modulates the strength of activation should allow us to differentiate between these interpretations.

It has been well established that prior experience with an object results in more efficient processing (i.e. repetition priming), and a reduced hemodynamic response – typically referred to as repetition suppression – when that object is encountered at a latter time (see Grill-Spector *et al.*, 2006, for recent review of neural models of repetition suppression). Recent studies have documented the usefulness of using repetition paradigms – also referred to as adaptation paradigms – for evaluating the processing characteristics of select brain regions (Grill-Spector & Malach, 2001). Within a region, if the responses to both the preferred and non-preferred category are informative, then both responses should be reduced with repetition. If the response to only the preferred category is informative, then a repetition-related reduction in hemodynamic response should be found for only the preferred category.

To evaluate these possibilities, subjects were given experience in naming and performing other tasks with sets of animal and tool pictures. Four days later they were scanned while silently naming these pictures and pictures of animals and tools they had not previously seen (Chao *et al.*, 2002). The results provided evidence that both views may be correct, depending on region and category.

Within the ventral object processing stream, responses to both preferred and non-preferred categories were reduced with experience. The lateral region of the fusiform gyrus, defined by a greater response to naming animals than tools, showed a reduced response to previously named animals and tools, relative to those not seen before. The medial region of the fusiform gyrus, defined by a greater response to naming tools than animals, showed an experience-related reduction in response to both object categories, as well (see Avidan *et al.*, 2002 for similar findings).

In contrast, other regions (right STS, left MTG, left intraparietal, and ventral premotor cortices) showed reduced hemodynamic responses only to the preferred category. For example, as in our previous studies, naming tools elicited a stronger response in ventral premotor cortex than naming animals. Although the response to naming animal pictures was significantly above baseline, this response was equivalent for both new and old animal pictures (i.e. no repetition suppression effect). This result was interpreted as consistent with the sensory—motor account of concept organization. If information about how objects are used is represented in parietal and premotor areas, then responses in these regions should be associated only with objects that are typically manipulated (i.e. tools, not animals). A major implication of these findings is that the presence of a significant hemodynamic response does not, in and of itself, indicate whether that response is meaningful. In each case, evidence will be needed to show that the response can be experimentally modulated in a predictable fashion.

Given these findings, I shall now discuss a series of studies aimed at addressing particular questions and concerns about the organization of conceptual knowledge in the brain as revealed by functional brain imaging.

12.10 Is activity in the fusiform gyrus related to conceptual processing?

I have suggested that category-related activity in the fusiform gyrus and elsewhere in ventral object processing stream reflects, in part, the automatic retrieval of stored information about object form properties necessary to identify objects quickly and efficiently. Furthermore, I have argued that this information is accessed regardless of the physical nature of the stimulus used to represent the object. Support for this notion comes from studies that have presented objects in the form of their written names, rather than as pictures. Alternatively, it could be argued that these activations do not reflect conceptual processing, *per se*, but rather the explicit retrieval of visual object imagery that accompanies task performance. Thus one could argue that the words in these tasks triggered visual imagery, which then recruited ventral occipitotemporal cortex indirectly, rather than this area doing any conceptual work. Indeed, fusiform gyrus activity has been

associated with object imagery (Ishai *et al.*, 2000; O'Craven & Kanwisher, 2000), word imageability (Wise *et al.*, 2000), imagery associated with property verification tasks (Kan *et al.*, 2003) and with the generation of mental images from spoken words relative to passive listening (D'Esposito *et al.*, 1997).

As noted previously, repetition suppression effects can be used to evaluate learning-related changes in specific regions of the cortex. To address this important concern about explicit visual image generation we sought to determine if automatic semantic priming is associated with a repetition suppression. In an automatic semantic priming paradigm, word pairs are presented using a short stimulus-onset asynchrony (SOA, the time from the onset of the first word in a pair to the onset of the second word). We reasoned that modulations associated with automatic semantic priming would occur too quickly to be reasonably ascribed to explicit visual image generation. Thus finding repetition suppression effects due to reading semantically related word pairs would add considerable weight to the claim that these regions are involved in conceptual representation. In our study, we presented word pairs consisting of the names of unrelated (apple–lion), semantically related (chair–bed), and identical (dog–dog) objects. The duration of the word pairs was 400 ms (150 ms per word with a blank 100 ms inter-stimulus interval (ISI), yielding a 250 ms SOA). We identified all of the brain regions that were active when subjects read the word pairs, and then investigated the pattern of activity in these regions associated with the different word pair types (unrelated, semantically related, identical). Repetition-related reductions in hemodynamic responses (i.e. repetition suppression) was observed in several regions, prominently including the fusiform gyrus. Activity in the fusiform gyrus was greatest for unrelated pairs, less for semantically related pairs, and least for the same-word repetitions, mirroring the pattern of behavioral performance based on reading times for the second word in each pair (slowest for unrelated, faster for related, and fastest for identical words; Wheatley *et al.*, 2005) (Figure 12.3). Thus the fusiform gyrus, and other regions (left prefrontal cortex) were sensitive to object meaning, even when neither explicit selection nor retrieval of semantic information was required. Moreover, because of the extremely short duration between word pairs, these data seem to rule out the possibility that fusiform activity was due to the explicit generation of visual object images.

It is important to stress that I am not suggesting that visual imagery (i.e. retrieving stored information about what an object looks like) played no part in producing the pattern of results we observed in this and other studies. To the contrary, I would argue that it was the retrieval of visual information about the objects that was primarily responsible for the activations we observed in the fusiform gyrus. However, it is assumed that this visual object information

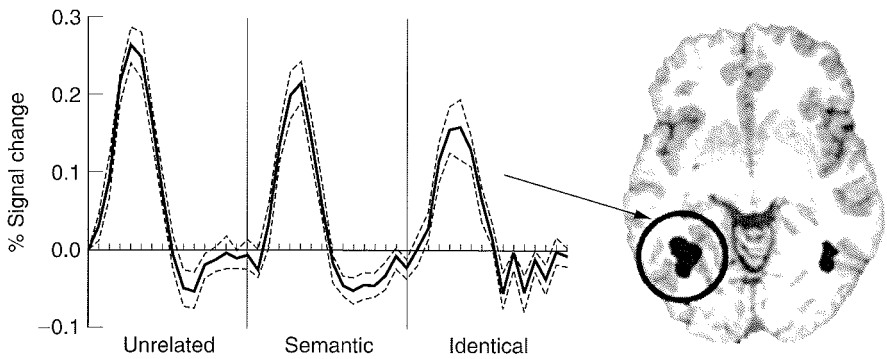


Figure 12.3. Modulation of neural activity associated with automatic semantic priming. Group averaged hemodynamic response from the region of left fusiform gyrus identified by comparing all word pair conditions to visual fixation. Dashed lines indicate ± 1 SEM. Axial slice shows location of the activation. Adapted from Wheatley *et al.* (2005).

is automatically retrieved as an unconscious and obligatory byproduct of normal reading of concrete nouns. In that case, automatic, implicit generation of an object image would be the mechanism by which we access an important property underlying the meaning of words denoting concrete entities (i.e. information about what the object looks like). In this sense, implicit visual imagery would be an obligatory component of reading for meaning. The main point here is that these data argue against the idea that activation of the fusiform gyrus during conceptual processing tasks can be readily explained by the non-obligatory, explicit generation of visual object images that occurred after the word's meaning had been determined (and see Gold *et al.*, in press, for a recent replication of repetition suppression in the fusiform gyrus by automatic semantic priming).

12.11 Are these neural circuits involved in learning about object property information?

Within the context of the sensory–motor model outlined here, differential activation of the medial fusiform gyrus, left MTG, intraparietal, and ventral premotor regions represent automatic retrieval of information about form, motion, and use-associated motor skills, respectively, of man-made manipulable objects such as common tools. It is further assumed that this information is necessary for the rapid and efficient identification of objects from this superordinate category. If so, then it should be possible, in principle, to elicit activity in these regions, *de novo*, as a result of experience with novel objects.

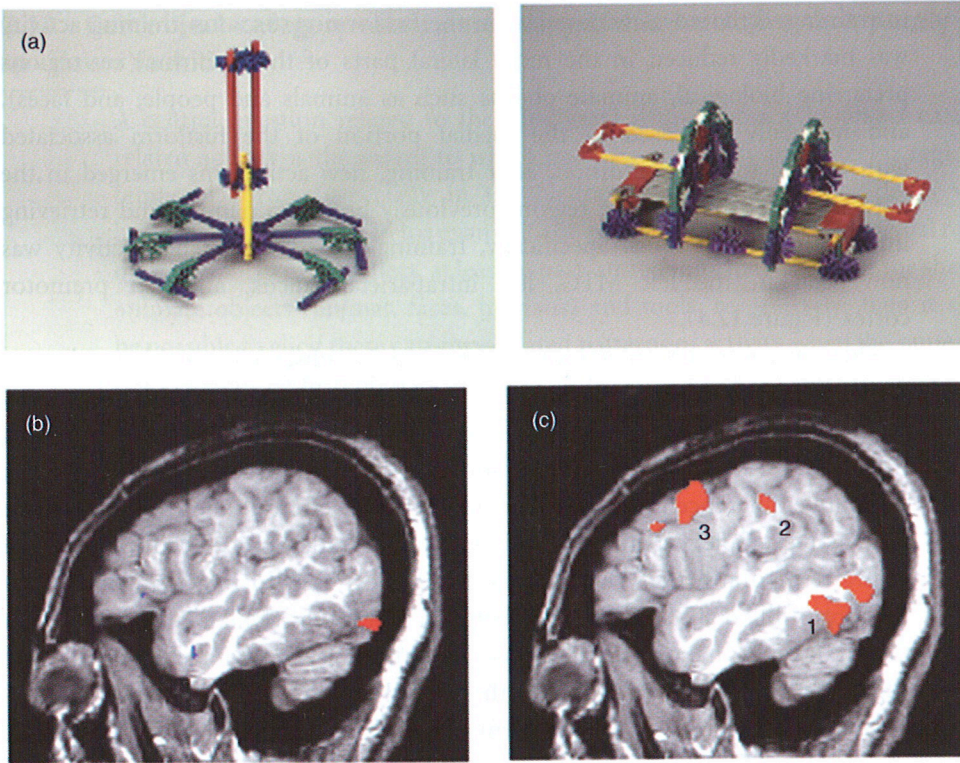


Figure 12.4. (A) Examples of novel objects. Left lateral view of a single subject (A) prior to training, and (B) after extensive training to use the novel objects to perform specific functional tasks. 1. MTG; 2. intraparietal sulcus. 3. ventral premotor cortex. Adapted from Weisberg *et al.* (in press).

To address this possibility, we created a set of 32 novel objects (Figure 12.4) (Weisberg *et al.*, in press). Although they do not look like tools, each object could be used to perform a specific, tool-like task. Subjects were given extensive experience performing functional tasks with 16 of these objects (three 90-minute sessions, over a 10-day period). Subjects were scanned, prior to and after training, while performing a simple visual matching task with pictures of the objects taken from different views, and with phase-scrambled images of the objects.

The critical question was: how did the pattern of activity associated with viewing these objects change after subjects had received extensive experience using them as tools? Prior to training, performing the simple visual matching task elicited activity in the posterior ventral cortex, consistent with previous reports on viewing non-meaningful objects (e.g. van Turennout *et al.*, 2000). However, after training, a very different picture remerged. First, activations in ventral cortex became more focal. Specifically, whereas prior

to training, activity was widespread in the fusiform gyrus, after training activity was markedly reduced in the more lateral parts of the fusiform (i.e. regions preferring biological, animate objects such as animals and people, and faces), and markedly increased in the medial portion of the fusiform associated with known tools. In addition, after training, new activations emerged in the network of left-hemisphere regions previously linked to naming and retrieving information about tools. Specifically, training-related, heightened activity was now seen in the left MTG, left intraparietal sulcus, and left premotor cortex (Figure 12.4).

Thus, in contrast to repetition suppression, we observed repetition enhancements (Desimone, 1996; Henson, 2003). Moreover, these enhancements occurred in regions linked to perceiving and knowing about common tools. Previous studies have suggested that repetition enhancement occurs when there is a qualitative difference in the way an object is perceived from one repetition to the next. For example, repetition of ambiguous, degraded objects led to increased ventral temporal activity when subjects were exposed to intact, unambiguous versions of the objects interspersed between repetitions (Dolan *et al.*, 1997). In a similar fashion, hands-on experience with the objects in our study may have augmented their representations with detailed information about their appearance (medial portion of the fusiform gyrus), and with information about the motion (middle temporal gyrus) and motor-related properties (parietal and premotor cortices) associated with their use. As a result, objects perceived as meaningless during the first scanning session were now perceived as objects with distinct functional properties. Thus the training interspersed between scanning sessions transformed the representation of these objects, leading to heightened activity from one scanning session to the next. Moreover, this heightened activity occurred in circumscribed regions associated with tools and their use, each of which is presumed to store information about perceptual or functional object properties.

These findings are consistent with the idea that we possess specialized neural circuitry for learning about specific sensory- and motor-related properties associated with an object's appearance and use (Santos *et al.*, 2003). Furthermore, the fact that this network was automatically engaged when perceiving the novel objects following training suggests that one role of these specialized systems may be to allow the organism to acquire information about the properties critical for identifying a category of objects, and to use this information in order to discriminate among them quickly and efficiently (Mahon & Caramazza, 2003). Moreover, our findings show that the locus of learning-related cortical plasticity appears to be highly constrained by both the nature of the information to be learned, and how it is acquired.

12.12 Can object category-related neural systems be active in a purely top–down fashion?

A central question related to the functional neuroanatomy of object category-related activity is the extent to which patterns of activity in posterior regions of temporal cortex (especially in the fusiform gyrus) reflect top–down versus bottom–up processes. If, for example, the activations in lateral and medial regions of the fusiform gyrus reflect, at least in part, stored information about the shapes of animate objects (animal, faces, humans) and tools, respectively, then it should be possible to elicit these category-related patterns of activity when the same visual objects are used to represent animate entities and artifacts. This would eliminate the concern that these category-related activations were solely due to bottom–up processing of visual differences in the shape or color of the stimuli used to represent them.

To address this question, we developed a set of animations composed of simple geometric forms in motion (Martin & Weisberg, 2003). The study was modeled after the now-classic demonstration by Heider and Simmel (1944) that simple geometric forms in motion can be interpreted, with little effort, as depicting animate beings with specific goals and intentions. Subjects were shown animated vignettes designed to elicit concepts related to social interactions (e.g. children playing baseball, sharing ice cream) or mechanical devices (a factory conveyor belt, a pin-ball machine). The same geometric forms were shown in random motion and in static displays for control conditions. The results showed the same dissociation in ventral and lateral temporal cortices as seen for animate objects and artifacts (Figure 12.5). In ventral temporal cortex, vignettes interpreted as conveying social interactions elicited heightened activity in the lateral fusiform gyrus, while the mechanical vignettes led to heightened activity in the medial fusiform gyrus. In lateral temporal cortex, the social vignettes elicited bilateral activation of STS (stronger in the right than left hemisphere), as typically seen with animate objects, whereas the mechanical vignettes elicited activity in left MTG, as typically seen for tools. Because the same geometric forms were used in both the social and mechanical animations, these results cannot be due to bottom–up processing of the visual stimuli. They must reflect top–down influences.

Interpreting the social vignettes also elicited activity in several regions associated with social and affective processes (e.g. Adolphs, 2001). Specifically, greater activity for social than mechanical vignettes was found in anterior regions of STS, the amygdala, and in ventromedial prefrontal cortex, all strongly lateralized to the right hemisphere (Figure 12.5). Thus these regions can be activated by stimuli that, in and of themselves, have neither affective valence nor

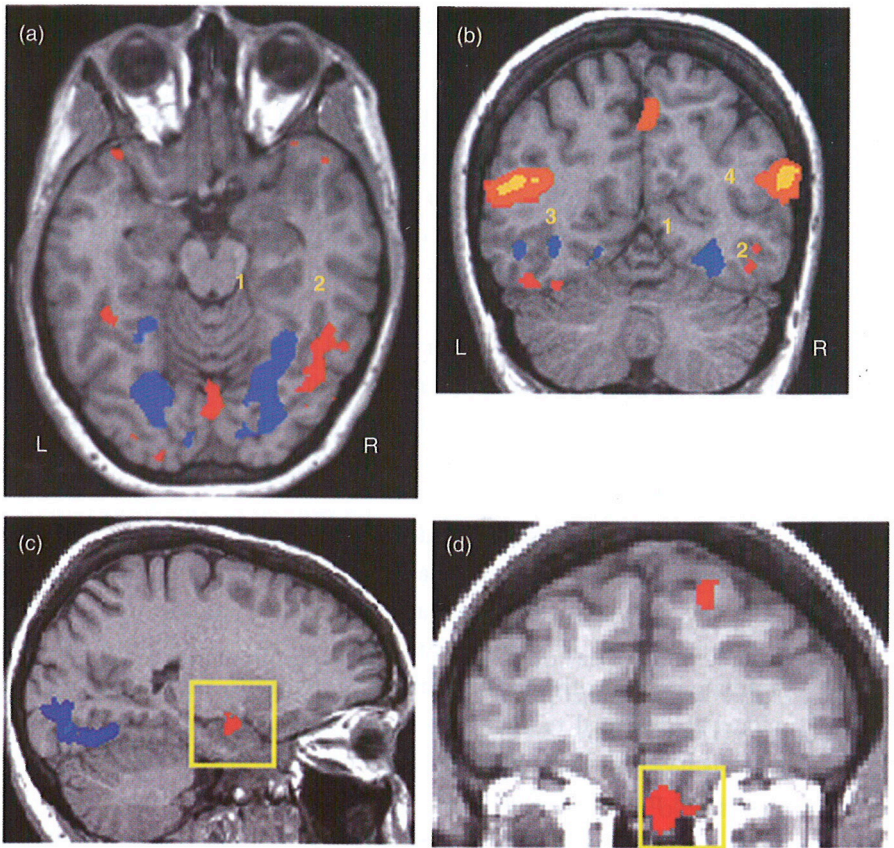


Figure 12.5. Group fMRI activation map showing axial view (A), and coronal view (B) of regions with greater activity associated with social (red) and mechanical (blue) interpretations of moving geometric forms. 1. Medial fusiform gyrus; 2. Lateral fusiform gyrus; 3. MTG, 4. STS. (compare to Figure 12.1). Yellow squares indicate right amygdala (C) and ventromedial prefrontal region (D) more active for social than mechanical vignettes. Adapted from Martin and Weisberg (2003).

social significance. The findings associated with the social vignettes closely replicated and extended the findings reported by Castelli and colleagues (Castelli *et al.*, 2000) and Shultz and colleagues (Schultz *et al.*, 2003) using a different set of animations that more closely resemble the original Heider and Simmel stimuli. By including the mechanical condition in our study, we were able to distinguish between regions associated with specific conceptual domains (social, mechanical) from those involved in the more general-purpose, problem-solving aspects of the tasks. These findings suggest that a higher-order concept like “animacy” may be represented in a network of regions composed of areas that store knowledge of what animate objects look like (lateral fusiform gyrus), how they move (STS),

coupled with areas for representing and modulating affect (amygdala and ventromedial frontal cortex). In this way, a property-based framework can provide the foundation or building blocks for realizing a large variety of basic object, as well as higher-order conceptual representations. A network dedicated to processing within the social domain is consistent with a domain-specific account, as well. Specifically, the data are consistent with the argument that natural selection has equipped us with a dedicated neural system for quick and efficient problem solving within the social domain.

12.13 Concluding comments

The evidence reviewed in this chapter suggests that we have dedicated neural circuitry for perceiving and knowing about animate agents and common tools. For animate agents, this circuitry includes two regions in posterior temporal cortex: the lateral portion of the fusiform gyrus and the STS. In addition, evidence is mounting that the amygdala also plays a prominent role in this circuitry, perhaps as a means of alerting the organism to a potentially threatening predator or prey (Yang *et al.*, 2005). Other regions, such as medial prefrontal cortex, may also be prominently involved when retrieving information about others (e.g. Mitchell *et al.*, 2002). For common tools, the neural circuitry includes the medial portion of the fusiform gyrus, as well as MTG, intraparietal sulcus, and premotor cortex, all within the left hemisphere.

In addition to the studies and evidence discussed in this chapter, findings from a large number of laboratories have provided evidence for other examples of domain-specificity in this region of the brain. This work includes studies showing that a region of the parahippocampal cortex is particularly responsive to depictions of places (outdoor scenes, buildings) and, on a more conceptual level, to objects strongly associated with spatial contexts (Bar & Aminoff, 2003). In addition, consistent with the idea that visual form is represented in ventral temporal cortex, there is mounting evidence for a region specialized for processing letter strings (the visual word form area, VWFA; Polk & Farah, 1998; Cohen *et al.*, 2000). Thus, rather than being a homogeneous, general object processing system, ventral occipital–temporal cortex has a distinct organization. Moreover, and perhaps most surprisingly, the spatial layout of these category-related regions is highly consistent from one subject to another. How to account for this consistency is a particularly challenging problem for future investigations. On the one hand, this consistently suggests the operation of strong, and perhaps genetically determined, constraints. On the other hand, the existence of a visual word form area provides equally strong argument against

genetic influences. After all, how could we be predisposed to develop a brain region specialized to accomplish a task — reading — that was only invented about 5500 years ago? One solution to this difficult problem is to suppose that the VWFA performs a visual processing function that predisposed it to being co-opted for reading. On this view, all of the so-called “category-related regions” discussed in this chapter presumably perform some as yet unspecified visual processing function that made them particularly well suited to process and store information associated with different object categories. The suggestion here is that the origin of these processing biases may be related to bottom–up features of the visual processing system (e.g. retinotopic organization; Malach *et al.*, 2002), and/or physical features of the stimuli themselves (e.g. spatial frequency, curvy versus angular forms, etc.). Top–down influences also likely play a prominent role in the form of predetermined connections between regions of occipitotemporal cortex and other brain areas. For example, the lateral regions of the fusiform gyrus may have developed its role in perceiving and storing information about animate objects due to privileged access to information from the amygdala (see Freese & Amaral, 2005, for evidence for direct feedback connections in the monkey from the amygdala to posterior regions of temporal and occipital cortex). In a similar fashion, the medial parts of the fusiform gyrus may receive privileged access to information about object manipulation from intraparietal and premotor regions, the parahippocampal area may received privileged access from parietal regions concerned with spatial vision, and the VWFA may have developed its role in reading due, in part, to privileged access to information originating in frontal and temporal regions that support language. Thus the possibility that different regions of ventral occipitotemporal cortex receive privileged bottom–up and top–down inputs may provide important clues to understanding the organization, and development, of object category-related regions in ventral temporal cortex.

Many questions remain to be resolved about the organization of neural systems supporting the expression of conceptual knowledge. Prominently included in that list will be a better understanding of how the nodes of the neural systems described in this chapter are bound together (e.g. Damasio, 1989), and how activity within the network is coordinated in the service of conceptual processing (Kraut *et al.*, 2002). An understanding of how category-related information links with lexical information and with other brain regions involved in supporting more general conceptual and semantic processes (e.g. left anterior temporal and inferior frontal cortices) is also lacking. Equally important will be to identify the neural systems that house the encyclopedic and associative object knowledge mentioned at the beginning of this chapter. In this regard, it is assumed that the neural systems

discussed here provide the foundation or scaffolding that allowed this information to be acquired in a fast and efficient manner.

One great advantage of functional imaging studies of the human brain is that it provides a means of not only identifying regions involved in performing a particular task, but also designing studies to probe the processing characteristics of each of those regions (e.g. testing hypotheses about the sensitivity of different regions of lateral temporal cortex to different types of object-associated motion; Beauchamp *et al.*, 2002, 2003). Nevertheless, it is important to note that the labels I've applied to the regions discussed in this chapter should be viewed only as place holders awaiting a much more precise and useful description of the role that these regions play in perceptual and conceptual information processing and storage. Future studies using high-resolution brain imaging and electrophysiological recordings in human and nonhuman primates offer the promise that this goal may be in reach.

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